Genetic analysis of carcass traits in beef cattle using random regression models

Englishby, TM; Banos, G; Moore, KL; Coffey, MP; Evans, RD; Berry, DP

Published in:
Journal of Animal Science

DOI:
10.2527/jas.2015-0246

Print publication: 01/01/2016

Document Version
Peer reviewed version

Random regressions for carcass traits in beef cattle

Genetic analysis of carcass traits in beef cattle using random regression models

T.M. Englishby,§† G. Banos,§ K.L. Moore,§ M.P. Coffey,§ R.D. Evans,‡ D.P. Berry†[2]

§Scotland's Rural College (SRUC), Easter Bush, Midlothian, EH25 9RG, United Kingdom; ‡Irish Cattle Breeding Federation, Bandon, Co. Cork, Ireland; and †Animal & Grassland Research and Innovation Centre, Teagasc, Moorepark, Co. Cork, Ireland

[1]*This study has been supported under the Teagasc Walsh Fellowship Scheme.*

[2]Corresponding Author: Donagh.Berry@teagasc.ie

Abstract

Livestock mature at different rates depending in part on their genetic merit; therefore, the optimal age at slaughter for progeny of certain sires may differ. The objective of the present study was to examine sire-level genetic profiles for carcass weight, carcass conformation and carcass fat, in cattle of multiple beef and dairy breeds, including crossbreeds. Slaughter records from 126,214 heifers and 124,641 steers aged between 360 and 1200 days, and from 86,089 young bulls aged between 360 and 720 days, were used in the analysis; animals were from 15,127 sires. Variance components for each trait across age at slaughter were generated using sire random regression models that included quadratic polynomials for fixed and random effects; heterogeneous residual variances were assumed across ages. Heritability estimates across genders ranged from 0.08 (± 0.02) to 0.34 (± 0.02) for carcass weight, 0.24 (± 0.02) to 0.42 (± 0.01) for conformation and 0.16 (± 0.03) to 0.40 (± 0.02) for fat score. Genetic correlations within each trait across ages weakened as the interval between ages compared lengthened, but were all >0.64 suggesting a similar genetic background for each trait across different

ages. Eigenvalues and eigenfunctions of the additive genetic covariance matrix revealed genetic variability among animals in their growth profiles for carcass traits although most of the genetic variability was associated with the height of the growth profile. At the same age, a positive genetic correlation (0.60 to 0.78; standard errors ranged from 0.01 to 0.04) existed between carcass weight and conformation, whereas negative genetic correlations existed between fatness and both conformation (-0.46 to 0.08; standard errors ranged from 0.02 to 0.09) and carcass weight (-0.48 to -0.16; standard errors ranged from 0.02 to 0.14) at the same age. The estimated genetic parameters in the present study indicate genetic variability in growth trajectory in cattle which can be exploited through breeding programmes and used in decision support tools.

Keywords: cattle, carcass weight, conformation, fat, Legendre polynomials, random regression

INTRODUCTION

Animals develop and mature at different rates depending on their genetic merit (Marshall, 1994; Robinson, 1996). Therefore progeny of some animals may reach the desired carcass weight, conformation, and subcutaneous fat level specified by abattoirs at different ages. As these traits are the most economically important in beef cattle production, knowledge of the optimum age at which an animal is likely to be suitable for slaughter is desirable. High heritability of various carcass characteristics in cattle have been documented (Hickey et al., 2007; Pabiou et al., 2011a) and thus genetic merit of the individual is likely to have a strong impact on such characteristics.

Random regression models (RRM) are widely used in the dairy industry to model lactation profiles (Jamrozik et al., 1998; Cobuci et al., 2005). Random regressions have

also been used in the study of growth on a live weight basis, using multiple measures recorded over time (Meyer, 2001; Coffey et al., 2006). Random regression models have not, however, been used in the study of carcass traits since these are end-of-life traits measured only once in an animal's lifetime. It is, nonetheless, possible to longitudinally model a trait for different sires exploiting information on the relatedness among progeny slaughtered at different ages, thereby providing several effective measurements per sire across a time trajectory (Jones et al., 1999).

The objective of the present study was to examine sire genetic profiles for three carcass traits namely carcass weight, carcass conformation and carcass fat across different ages of progeny slaughtered. Knowledge of the genetic variability in the trajectory for carcass traits could facilitate more informed selection and management decisions such as penning of animals with expected similar growth patterns.

MATERIALS AND METHODS

All data used in the present study were obtained from the Irish Cattle Breeding Federation (ICBF) database.

Data

Carcass weight (kg), carcass conformation (scale 1 to 15; Table 1) and carcass fat score (scale 1 to 15; Table 1) records from 5,223,983 singleton animals from 101,171 Irish herds slaughtered between the years 2010 and 2013 were available. Carcass weight is measured on average two hours after slaughter following the removal of the head, legs, thoracic and abdominal organs, and internal fats and hide. In Ireland, carcass conformation and fat scores are graded using Video Image Analysis (Pabiou et al.,

2011b). The resulting EUROP classification grades were transformed into a 15-point numeric scale outlined in Table 1.

Records were removed for animals that moved herd more than once during their lifetime. The remaining 1,319,863 records were restricted to animals slaughtered >360 days or <1200 days of age. Cows (i.e., females that had at least one recorded calving date) and mature bulls >720 days of age at slaughter were not further considered, nor were animals with no recorded sire or dam. Furthermore, records more than four standard deviations from the within gender population mean carcass weight or age at slaughter were also discarded. Only carcass weight records between 120 kg and 543 kg, between 120 kg and 577 kg, and between 136kg and 577 kg were retained for heifers, steers and young bulls, respectively. Dam parity was restricted to 1 to 10 and parity was subsequently categorized as 1, 2, 3, 4, and ≥5. Only progeny from sires with at least 5 paternal half-sibs with records were retained. Following these edits, 541,595 carcass records remained.

Two contemporary groups were generated: 1) herd-year-season-gender of slaughter and 2) abattoir-date of slaughter. Gender in the present study refers to heifer, steer, or young bull. An algorithm was used to maximize the size of the herd-year-season-gender of slaughter contemporary group while simultaneously minimizing the duration of the contemporary group in time; this algorithm has been described in detail for genetic analyses of other animal traits in Irish genetic studies (McHugh et al., 2011; Berry and Evans, 2014). No contemporary group was longer than 60 days in duration and only contemporary groups with at least five records were retained. Following edits, 336,944 animals from 27,417 herd-year-season-gender contemporary groups in 9,572 herds remained. Of this dataset, 126,214 (37.5% of the data) were heifers, 124,641 (37% of the data) were steers and 86,089 (25.5% of the data) were young bulls. Animals

included in the analysis were from 15,127 sires. The pedigree of each animal was traced back to founder populations which in turn were allocated to genetic groups. The pedigree file consisted of 88,324 animals.

Data Analysis

Variance components for carcass weight, conformation and fat score were estimated for each gender separately using sire RRM in AsReml (Gilmour et al., 2009). The data of young bulls were divided into nine groups based on age at slaughter as 360-400, 401-440, 441-480, …., 681-720 days. Heifer and steer data was divided into 21 groups as 360-400, 401-440, 441-480, …., 1161-1200 days. Residual variances were assumed to be homogenous within each age class but heterogeneous between each age class. The number of animals in each residual class is in Table 2.

The fitted model was

$$Y_{dhjklqnz} = Parity_d + Abattoir - DoS_j + \sum_{h=1}^{9} c_h \,.\, Dambreed_h + a_1 \,.\, Het + a_2 \,.\, Rec + \sum_{i=1}^{n} b_n P_n Age + \sum_{i=1}^{n} Sire_{kn} P_n Age + \sum_{i=1}^{n} HY_{ln} P_n Age + HYS_q + e_{dhjklqnz} \quad (1)$$

where $Y_{dhjklqnz}$ = the observed carcass weight, carcass conformation class or carcass fatness class on animal *z*; $Parity_d$ = the fixed effect of the d^{th} parity of the dam of animal *z* (5 levels); $Abattoir\text{-}DoS_j$ = fixed effect of date of slaughter *j* (12,251 levels); c_h = partial regression coefficients on proportion of breed of the dam (Dambreed) *h* summed over all breeds (sum of proportion across the 9 breeds equals to unity); a_1 = linear regression coefficients on heterosis (Het) in animal *z*; a_2 = linear regression coefficients

on recombination loss (Rec) in animal z; Age = age at slaughter; b_n = fixed regression coefficient on age at slaughter; P_n = nth order Legendre polynomial of age at slaughter; $Sire_{kn}$ = random regression coefficient on age at slaughter associated with the genetic effect of sire k of animal z; HY_{ln} = random regression coefficient on age at slaughter associated with the effect of gender finishing herd-year of slaughter l; HYS_q = the random effect of gender finishing herd-year-season of slaughter q; n =the order of Legendre polynomial; $e_{dhjklqnz}$ = the residual error term for age class modelled as heterogeneous across age.

The most parsimonious fixed effect Legendre polynomial regression was based on both the F-statistic of the higher order polynomial terms but also by visual comparison of the resulting profile for the different model orders. In all instances a quadratic fixed effect polynomial was most appropriate. Although a higher order polynomial fitted the data better ($P<0.05$), the profiles of the quadratic and higher order polynomials were visually identical. The decision of the most parsimonious order of random Legendre polynomial regression on sire was based on the Akaike's Information criterion (AIC) with the fixed effects in the model being consistent across models compared.

Genetic covariance function coefficients were estimated as

$$\delta^2 = \Phi' K \Phi$$

Where δ^2 is the variance (co)variance matrix for slaughter ages, Φ is the matrix of Legendre polynomial age regression coefficients, and K is the estimated variance covariance matrix of the random polynomial coefficients multiplied by four to transform from a sire variance to a genetic variance (Huisman et al., 2002). Standard errors of the heritability estimates were derived using a Taylor series expansion (Fischer et al., 2004).

Genetic correlations between carcass weight, conformation and fat score at each age were estimated using a series of bivariate RRM analyses in AsReml (Gilmour et al., 2009). Fixed and random effects included in the models were as described for the univariate analyses (model 1). The inability of bivariate models to converge when a higher order of random regression was fitted necessitated the order of the fitted random regression to be linear. Residual variances were estimated within each age class as described for the univariate analysis, and a residual covariance between traits was assumed within residual age classes.

Standard errors of genetic correlations were estimated using (Falconer and MacKay, 1996):

$$\sigma_{(r_A)} = \frac{1 - {r_A}^2}{\sqrt{2}} \sqrt{\frac{\sigma_{(h_x^2)}\, \sigma_{(h_y^2)}}{h_x^2\ h_y^2}}$$

Where σ denotes the standard error, r_A is the genetic correlation between trait *x* and trait *y,* and h^2 is the heritability; the superscript *x* or *y*, represent the respective traits under investigation.

Eigenvalues and eigenvectors were calculated from singular value decomposition of the additive genetic covariance matrix, and eigenfunctions were subsequently calculated from the product of the eigenvectors and Legendre polynomial coefficients as:

$$\Psi_i(x) = \sum_{j=0}^{p-1} [k_{\Psi_i}]_j \, \emptyset_j(x)$$

Where $[k_{\Psi_i}]_j$ is the j^{th} element of the i^{th} eigenvector of *K*, Φ is the j^{th} polynomial relating to the p^{th} order of fit, and *x* is age of slaughter.

RESULTS

The frequency distribution at age of slaughter for young bulls, steers and heifers is in Figure 1. A total of 96.6% per cent of the young bulls were slaughtered between the ages of 420 and 720 days. A total of 84.8% of steers were slaughtered between 650 and 1010 days of age. Of the heifers slaughtered, 84.3% were slaughtered between the ages of 530 and 900 days. Therefore, to minimize the influence of data at the extremities of the parameter space on the fitted polynomials at the extremes, only (co)variance components between 420 and 720 days, 650 and 1010 days and 530 and 900 days are presented for young bulls, steers and heifers, respectively.

Descriptive statistics of carcass weight, conformation score, fat score and age at slaughter in each gender are in Table 3. Young bulls were slaughtered at an average age of 583 days and had a heavier mean carcass weight than steers and heifers. Young bulls also had the best conformation and were the leanest of the three genders. For all genders, carcass weight increased constantly as animals aged (Figure 2). Maximum conformation (i.e., age at point of inflection) was reached in steers and heifers at a similar age of 934 days and 938 days, respectively. In young bulls and steers, fat deposition increased as age at slaughter increased albeit, at a declining rate, whereas fat deposition reached maximum in heifers at 780 days.

Variance Components

A quadratic random Legendre polynomial on sire fitted the data best for all traits and genders. A quadratic random Legendre polynomial on herd-year also fitted the data best for all traits and genders. Residual variances were heterogeneous across age

197 (Appendix 1). Young bulls had greater residual variation for all three traits, except for
198 fat score, where the residual variance was greatest in heifers.
199 Genetic variances followed similar trends for all traits and genders, increasing as age at
200 slaughter increased (Figure 3). The ranges of genetic variance estimates were similar
201 across gender for carcass weight and conformation. Average genetic variance estimates
202 were greatest for fat score in steers (0.57 ± 0.04 units^2) whereas the least genetic
203 variation for fat score was observed among young bulls (0.16 ± 0.02 units^2).
204 Heritability estimates for carcass weight across ages of slaughter were greater in heifers
205 (0.17 ± 0.02 to 0.34 ± 0.02) and steers (0.21 ± 0.01 to 0.27 ± 0.01) than in young bulls
206 (0.08 ± 0.02 to 0.16 ± 0.01). Peak heritability for carcass weight corresponded to the
207 greatest estimates of genetic variation (Figure 4). Fat score was more heritable in
208 heifers than in steers and young bulls, ranging from 0.28 (±0.02) at 530 days of age at
209 slaughter to 0.39 (±0.02) at 880 days of age at slaughter. Heritability estimates for
210 conformation across genders increased as age of slaughter increased (Figure 4). This
211 increase was greatest in heifers, where heritability of conformation increased from 0.24
212 (±0.02) at 530 days of age at slaughter to 0.42 (±0.02) at 871 days of age at slaughter.
213 On average, conformation across age at slaughter and genders was the most heritable
214 trait 0.36 (± 0.01), whereas carcass weight across age at slaughter and genders was the
215 least heritable trait 0.23 (± 0.01).
216 The largest eigenvalues explained 81%, 90% and 95% of the genetic variation for
217 carcass weight in heifers, steers and young bulls, respectively. In all the models, the
218 largest proportion of the genetic variation was explained by the intercept term of the
219 RRM. The eigenfunctions associated with the largest eigenvalues for carcass weight,
220 conformation and fat were of the same sign across ages of slaughter in all genders
221 (Figure 5). Similar to carcass weight, the intercept term explained the majority of the

genetic variance for conformation (82%, 96% and 93% for heifers, steers and young bulls, respectively) and fat score (91%, 89% and 95% for heifers, steers and young bulls, respectively). Eigenfunction estimates relating to the second largest eigenvalues explained between 4% (conformation in steers) and 18% (carcass weight in heifers) of the genetic variability. The eigenfunctions corresponding to the second eigenvalues for carcass weight were the same sign across ages of slaughter in all genders except young bulls. The second eigenfunctions associated with conformation and fat were positive at early ages at slaughter and negative at older ages at slaughter in steers and young bulls (Figure 5).

Genetic correlations within trait

Within trait genetic correlations across different ages at slaughter ranged from 0.64 (± 0.02) to 1.00 (± 0.00) in heifers, from 0.94 (±0.01) to 1.00 (± 0.00) in steers, and from 0.74 (± 0.01) to 1.00 (± 0.00) in young bulls (Figure 6). Within trait correlations were strongest between adjacent ages, approaching unity, and weakened as the interval between ages lengthened. Across genders, within trait genetic correlations between youngest and oldest ages at slaughter were strongest for conformation scores and weakest for fat scores (Figure 6). The weakest genetic correlation 0.64 (± 0.02) was observed in heifers between carcass weight at 530 days and 900 days of age at slaughter.

Genetic correlations between traits

Irrespective of gender, genetic correlations between carcass weight and conformation at the same age at slaughter were strongly positive reaching a maximum correlation of 0.78 (± 0.04) in young bulls at 420 days of age at slaughter (Figure 7). In contrast,

247 estimates of the genetic correlations between carcass conformation and fat score at the
248 same age were negative. Genetic correlations between carcass weight and fat score
249 were negative at younger slaughter ages and became weaker as age at slaughter
250 increased. The weakest genetic correlation between carcass weight and fat was -0.48
251 (±0.02) at 597 days of age in heifers.
252 Strong positive to weak negative genetic correlations existed between carcass weight
253 and the two other carcass traits, while the genetic relationship between fat and
254 conformation varied around zero.
255
256 **DISCUSSION**
257 ***Modelling***
258 Growth curves that model both fixed and random effects are potentially a useful tool for
259 selective breeding but also for precision-based management. Carcass development has
260 mainly been modelled on a live weight basis using several different methods. These
261 approaches include non-linear growth functions such as von Bertalanffy (von
262 Bertalanffy, 1957), Gompertz (Winsor, 1932) and Brody (Brody, 1945), that describe
263 the relationship between weight and age (Berry et al., 2005) using parameters with
264 biological meaning. An additional approach includes multi-trait analyses considering
265 different ages as separate traits (Nobre et al., 2003). Random regression models have
266 previously been applied to growth studies where multiple live weight records
267 exist (Meyer, 2000; Legarra et al., 2004). Studies that use RRM in the analysis of carcass
268 growth are however, to our knowledge, non-existent. The present study used
269 covariance functions to model growth rather than the traditionally used growth
270 functions; an advantage of the former is that no prior assumptions about the shape of
271 the curve over time are required (Meyer and Hill, 1997). In addition, modelling the

272 covariance structure as a covariance function permits a gradual change in (co)variances
273 at different ages at slaughter. A benefit of this was that it facilitated the estimation of
274 covariance between ages for which no records necessarily existed (van der Werf et al.,
275 1998) but also between different carcass characteristics at different ages.
276 The RRM fitted in the present study used Legendre polynomials, a function that is
277 commonly used in the dairy industry to generate lactation profiles (Liu et al., 2003;
278 Mrode et al., 2003). Legendre polynomials are favoured because their orthogonal
279 properties assist with model convergence (Brotherstone et al., 2000; Bohmanova et al.,
280 2008); nonetheless, the fit may not be optimal at the extremes of the trajectory due to
281 the scarcity of data at the extremities and the mathematical properties of polynomials
282 (Legarra et al., 2004). The most parsimonious order of the polynomial term used,
283 however, varies across studies. Nobre et al. (2003) used cubic Legendre polynomials to
284 model growth curves in Nellore beef cattle, whereas, Arango et al. (2004) documented
285 that the additive genetic covariance structure of live weight in beef cows could be
286 described using linear random regression. The most parsimonious RRM in the present
287 study was third order (i.e., quadratic) Legendre polynomials for the fixed and both
288 random trajectories. Using equal orders of fixed and random effects have been
289 suggested in the literature (Pool et al., 2000). Furthermore the analysis of eigenvalues
290 of genetic covariance (Figure 5) for each trait, suggests the diminishing importance of
291 adding further polynomial terms in explaining the additive genetic variance effects.
292
293 ***Genetic parameters for carcass weight***
294 Carcass weight, which reflects lifetime growth, is a routinely evaluated trait in many
295 beef genetic evaluations (Pabiou et al., 2011b). The genetic parameter estimates
296 obtained in the present study using RRM corroborate those reported in other cattle

297 populations estimated using traditional linear models (Gregory et al., 1995; Kause et al.,
298 2015), including those from data on Irish cattle (Hickey et al., 2007; Pabiou et al., 2009;
299 Pabiou et al., 2011a). The average heritability for carcass weight across genders and age
300 at slaughter in the present study (0.23 ± 0.01) is similar to the estimate reported by
301 Hickey et al. (2007) in Irish beef cattle, estimated using a linear animal model with a
302 phenotypic adjustment for age. Hickey et al. (2007) reported varying direct heritability
303 estimates for carcass weight in cattle depending on breed composition, (0.17 for
304 Aberdeen Angus or Belgian Blue sired to 0.65 Simmental sired).
305 Eigenfunctions are continuous functions whose coefficients are formed by the
306 decomposition of the (co)variance matrices (Kirkpatrick and Heckman, 1989).
307 Eigenfunctions provide information on how growth trajectories may change in response
308 to selection (Meyer and Hill, 1997) and have previously been applied to live-weight
309 records in dairy cows (Berry et al., 2003). Analysis of the eigenvalues and
310 eigenfunctions of the additive genetic covariance matrices in the present study revealed
311 genetic variability does indeed exists among animals in their growth profiles for carcass
312 weight (Figure 5). Most of the genetic variance was however attributable to the
313 intercept which suggests that the greatest opportunity exists to alter the height of
314 growth profiles for carcass weight. This substantiates the strong positive genetic
315 correlation that existed for carcass weight across different ages or in other words,
316 selection for heavier carcass weights at any age would increase carcass weights at all
317 ages (Figure 6). The strong genetic correlations between carcass weight at different
318 ages corroborates documented genetic correlations from studies on live weight using
319 both RRM (Arango et al., 2004) and traditional linear models (McHugh et al., 2014),
320 where strong correlations existed between live weights at younger and older ages. The
321 change in sign of the second eigenfunctions for carcass weight across ages in steers and

young bulls, and in the third eigenfunctions in heifers and young bulls, provides evidence that exploitable genetic variation also exists in the shape of the growth curve (Figure 5). The genetic variation however was limited; therefore a greater weight would have to be imposed on the second and third eigenfunctions to alter the shape of the growth curves for carcass weight.

Generally in genetic evaluations of carcass traits, carcass weight at different ages is treated as the same trait (i.e., genetic correlation of unity among different ages) and age at slaughter adjustments are at the phenotypic level. The results in this present study mostly support this. Nonetheless, the existence of some moderate genetic correlations (i.e., as low as 0.64) between carcass weight in heifers between extreme ages suggests that, in fact carcass weight at extremely different ages in heifers may indeed be governed by different allelic variability. It has been proposed that genetic correlations of less than 0.80 may be different traits due to the existence of genotype-by-environment interactions and should therefore be treated as such (Robertson, 1959). Nonetheless, due to high computational requirements, the gain in accuracy of genetic evaluations may not justify the increased complexity of the genetic evaluation model that incorporates RRM.

Genetic parameters for carcass conformation and fat

While RRM have previously been used to model animal (live-) weight in cattle (Meyer, 2000; Coffey et al, 2006), the use of RRM to model animal conformation or fat are non-existent in beef cattle although it has been undertaken in dairy cattle (Coffey et al, 2001). As with carcass weight, the heritability estimates for conformation and fat score were within the ranges of those reported from traditional linear models in other international beef populations (Utrera and Van Vleck, 2004) and in Irish populations

(Hickey et al., 2007; Crowley et al., 2011; Pabiou et al., 2011a). Pabiou et al. (2011a), using data from Irish abattoirs, reported direct heritability estimates for conformation and fat score ranging from 0.28 to 0.46 and from 0.27 and 0.40, respectively from an animal linear mixed model. Similar to carcass weight, the constant positive eigenfunctions relating to the largest eigenvalues of conformation and fat indicate an opportunity to alter the height of conformation and fat profiles to suit specific breeding objectives (Figure 5) and substantiates the strong genetic correlations that exist within each trait at different ages. The change in sign of the second and third eigenfunctions between younger and older ages at slaughter in steers and young bulls suggests the presence of factors with opposing effects on conformation and fat across ages at slaughter. Response to selection based on the second and third eigenvalues would be slow as they account for only less than 18% of the additive genetic variation; therefore, altering the shape of the profile through breeding may prove difficult as greater selection pressure would have to be imposed on the second and third eigenfunctions for conformation and fat.

Genetic correlation between traits at the same age

Estimates in the literature (Gregory et al., 1995; Kause et al., 2015) of the genetic correlations among carcass weight, conformation and fat vary widely among populations. Such variability may be due to differences in breeds or analytical methods used in the different studies. Based on results from the present study, these apparent discrepancies among studies may also be due to differently aged animals being included in the analysis. In the present study, increasing carcass weight was favourably related to better shaped carcasses in all genders. These strong positive correlations are consistent with those reported in the literature from traditional linear models (Van der

372 Werf et al., 1998; Bouquet et al., 2010), but stronger than those reported from other
373 Irish populations (Hickey et al., 2007; Pabiou et al., 2011a). Underlying genetic
374 correlations influence the potential for change in carcass traits at different ages and will
375 also impact the optimal age at which an animal should be slaughtered. In the present
376 study, correlations between traits across age at slaughter and gender were sufficiently
377 different from unity, suggesting that heavier animals may also be more muscular and
378 leaner at different ages at slaughter (Figure 7). The alleles affecting carcass weight and
379 muscularity are different to those influencing fatness across ages at slaughter and
380 therefore direct selection for heavier carcasses alone across all ages at slaughter does
381 not necessarily have to result in fatter carcasses. Random regression analyses provide
382 genetic information for carcass traits across all ages at slaughter and have the potential
383 to be used in routine genetic analysis of carcass traits. Based on the genetic correlation
384 structure between carcass traits across the trajectory, different emphasis may be placed
385 in an index using information from different ages to facilitate optimal selection for
386 combinations of carcass weight, conformation and fat levels at specific ages.
387
388 ***Implications***
389 This study shows the genetic relationships among carcass traits across varying ages at
390 slaughter in a population of Irish beef cattle using RRM. Results illustrate the potential
391 to select on carcass trait trajectories and to alter growth curves to meet specific
392 breeding objectives. Knowledge of the variability in genetic potential for carcass growth
393 and both muscle and fat deposition is important in order to achieve genetic gain. Such
394 information may also be useful in management decision support tools to align the
395 management of animals more closely with their growth potential. For example, in a
396 feedlot production system, grouping animals based on individual genetic growth

397 profiles, as opposed to breed, may facilitate better management of resources. In
398 addition, such grouping may aid in decisions on when best to slaughter pens of animals.

LITERATURE CITED

Arango, J., and L. D. Van Vleck. 2004. Covariance functions and random regression models for cow weight in beef cattle. J. Anim. Sci. 82:54-67.

Berry, D. P., and R. D. Evans. 2014. Genetics of reproductive performance in seasonal calving beef cows and its association with performance traits. J. Anim. Sci. 92:1412–1422.

Berry, D. P., B. Horan, and P. Dillon. 2005. Comparison of growth curves of three strains of female dairy cattle. Anim. Sci. 80:151–160.

Berry, D. P., F. Buckley, P. Dillon, R. D. Evans, M. Rath, and R. F. Veerkamp. 2003. Genetic Parameters for Body Condition Score, Body Weight, Milk Yield, and Fertility Estimated Using Random Regression Models. J. Dairy Sci. 86:3704–3717.

Bohmanova, J., F. Miglior, J. Jamrozik, I. Misztal, and P. G. Sullivan. 2008. Comparison of random regression models with Legendre polynomials and linear splines for production traits and somatic cell score of Canadian Holstein cows. J. Dairy Sci. 91:3627–38.

Bouquet, A., M. N. Fouilloux, G. Renand, and F. Phocas. 2010. Genetic parameters for growth, muscularity, feed efficiency and carcass traits of young beef bulls. Livest. Sci. 129:38–48.

Brody, S. 1945. Bioenergetics and growth; with special reference to the efficiency complex in domestic animals. New York. Reinhold Publishing Co. xii 1023 pp.

Brotherstone, S., I. M. S. White, and K. Meyer. 2000. Genetic modelling of daily milk yield using orthogonal polynomials and parametric curves. Anim. Sci. 70: 407-415.

Coffey, M.P., Emmans, G.E. and S. Brotherstone. 2001. Genetic evaluation of dairy bulls for energy balance traits using random regression. Anim. Sci. 73:29-40.

Coffey, M. P., Hickey, J. and S. Brotherstone. 2006. Genetic aspects of growth of holstein-friesian dairy cows from birth to maturity. J Dairy Sci. 89: 322-329.

Cobuci, J. A., R. F. Euclydes, P. S. Lopes, C. N. Costa, R. D. A. Torres, and C. S. Pereira. 2005. Estimation of genetic parameters for test-day milk yield in Holstein cows using a random regression model. Genet. Mol. Biol. 83:75–83.

Crowley, J. J., R. D. Evans, N. Mc Hugh, D. A. Kenny, M. McGee, D. H. Crews, and D. P. Berry. 2011. Genetic relationships between feed efficiency in growing males and beef cow performance. J. Anim. Sci. 89:3372–81.

Falconer, D. S., T. F., Mackay, and R. Frankham. 1996. Introduction to quantitative genetics (4th edn). Longman. pp.316.

Fischer, M.T., A. R., Gilmour and J. H .J. van der Werf. 2004. Computing approximate standard errors for genetic parameters derived from random regression models fitted by average information REML. Genet. Sel. Evol. 36: 363-369.

Gilmour, A. R., B. J. Gogel, B. R. Cullis, and R. Thompson. 2009. ASReml user guide release 3.0. VSN International Ltd., Hemel.

Gregory, K. E., L. V Cundiff, and R. M. Koch. 1995. Genetic and Phenotypic (Co) Variances for Growth of Beef Carcass Traits and Purebred and Composite Populations of beef cattle. J. Anim. Sci. 73:1920–1926.

Hickey, J. M., M. G. Keane, D. A. Kenny, A. R. Cromie, and R. F. Veerkamp. 2007. Genetic parameters for EUROP carcass traits within different groups of cattle in Ireland. J. Anim. Sci. 85:314–21.

Huisman, A. E., R. F. Veerkamp, and J. A. M. Van Arendonk. 2002. Genetic parameters for various random regression models to describe the weight data of pigs. J. Anim. Sci. 80:575-582.

Jamrozik, J., G. Jansen, L. R. Schaeffer, and Z. Liu. 1998. Analysis of persistency of lactation calculated from a random regression test day model. Interbull Bull. 17:64–69.

Jones, H. E., I. M. S. White, and S. Brotherstone. 1999. Genetic evaluation of Holstein Friesian sires for daughter condition score changes using a random regression model. Anim. Sci. 68:467–475.

Kause, A, L. Mikkola, I. Strandén, and K. Sirkko. 2015. Genetic parameters for carcass weight, conformation and fat in five beef cattle breeds. Animal. 9:35–42.

Kirkpatrick, M., and N. Heckman. 1989. A quantitative genetic model for growth, shape, reaction norms, and other infinite-dimensional characters. J. Math.Biol. 27:429–450.

Legarra, A., I. Misztal, and J. K. Bertrand. 2004. Constructing covariance functions for random regression models for growth in Gelbvieh beef cattle. J. Anim. Sci. 82 :1564–1571.

Liu, Z., F. Reinhardt, and R. Reents. 2003. Genetic evaluation for somatic cell scores using random regression test-day model for a very large dairy cattle population. Interbull Bull. 31:88–91.

Marshall, D. M. 1994. Breed differences and genetic parameters for body composition traits in beef cattle. J. Anim. Sci. 72:2745–55.

Mc Hugh, N., R. D. Evans, P. R. Amer, A. G. Fahey, and D.P. Berry. 2011. Genetic parameters for cattle price and body weight from routinely collected data at livestock auctions and commercial farms. J. Anim. Sci. 89:29-39.

Mc Hugh, N., A. R. Cromie, R. D. Evans, and D.P. Berry. 2014. Validation of national genetic evaluations for maternal beef cattle traits using Irish field data. J. Anim. Sci. 92:1423–1432.

Meyer, K. 2000. Random regressions to model phenotypic variation in monthly weights of Australian beef cows. Livest. Prod. Sci. 65:19–38.

Meyer, K. 2001. Estimates of direct and maternal covariance functions for growth of Australian beef calves from birth to weaning. Genet. Sel. Evol. 33:487–514.

Meyer, K., and W. G. Hill. 1997. Estimation of genetic and phenotypic covariance functions for longitudinal or " repeated " records by restricted maximum likelihood. Livest. Prod. Sci . 47:185–200.

Mrode, R. A., G. J. T. Swanson, and M. F. Paget. 2003. Implementation of the test day model for production traits in the UK. Interbull Bull. 31:193–196.

Nobre, P. R. C., I. Misztal, S. Tsuruta, J. K. Bertrand, L. O. C. Silva, and P. S. Lopes. 2003. Analyses of growth curves of Nellore cattle by multiple-trait and random regression models. J. Anim. Sci. 81:918–926.

Pabiou, T., W. F. Fikse, A. Näsholm, A. R. Cromie, M. J. Drennan, M. G. Keane, and D. P. Berry. 2009. Genetic parameters for carcass cut weight in Irish beef cattle. J. Anim. Sci. 87:3865–76.

Pabiou, T., W. F. Fikse, P. R. Amer, A. R. Cromie, A. Näsholm, and D. P. Berry. 2011a. Genetic variation in wholesale carcass cuts predicted from digital images in cattle. Animal. 5: 1720-1727.

Pabiou, T., W. F. Fikse, A. R. Cromie, M. G. Keane, A. Näsholm, and D. P. Berry. 2011b. Use of digital images to predict carcass cut yields in cattle. J. Livest. Sci. 137: 130-140.

Pool, M. H., L. L. Janss, and T. H. Meuwissen. 2000. Genetic parameters of legendre polynomials for first parity lactation curves. J. Dairy Sci. 83:2640–2649.

Robertson, A. 1959. The sampling variance of the genetic correlation coefficent. Biometrics. 15:469–485.

Robinson, D. L. 1996. Estimation and interpretation of direct and maternal genetic parameters for weights of Australian Angus cattle. Livest. Prod. Sci. 45:1–11.

Utrera, A. R., and L. D. Van Vleck. 2004. Heritability estimates for carcass traits of cattle: a review. Genet. Mol. Res. 3:380–94.

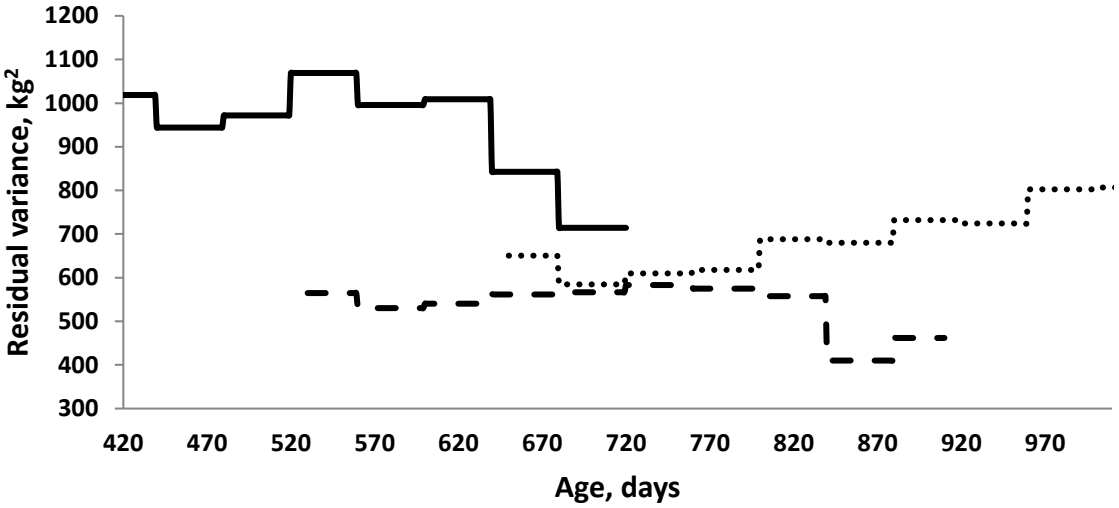
van der Werf, J. H. J., M. E. Goddard, and K. Meyer. 1998. Theuse of covariance functions and random regression for genetic evaluation of milk production. J. Dairy Sci. 81:3300–3308.

Von Bertalanffy, L. 1957. Quantitative laws in metabolism and growth. Q. Rev. Biol. 32:217–231.

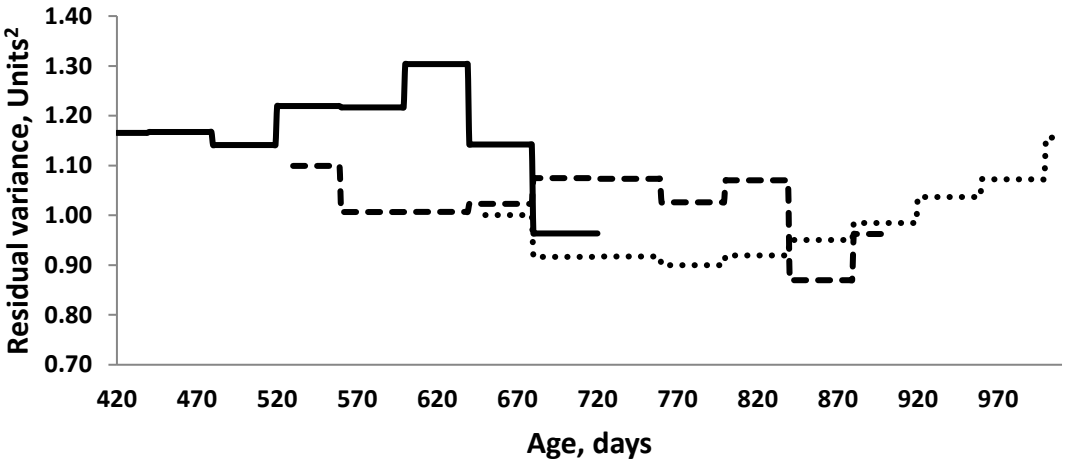
Winsor, C. P. 1932. The Gompertz Curve as a Growth Curve. Proc. Natl. Acad. Sci. 18:1-8.

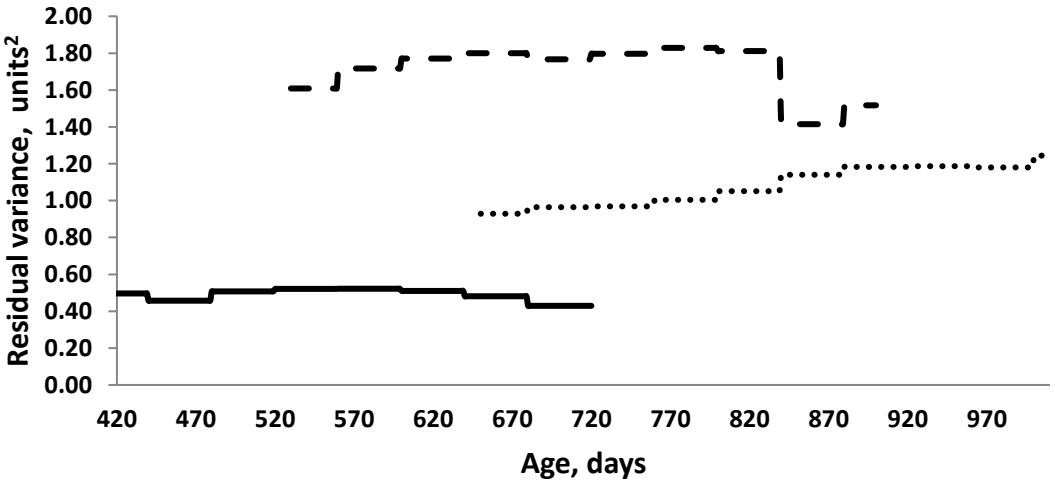
APPENDIX 1 : RESIDUAL VARIANCE ESTIMATES

(a)



(b)





Estimates of residual variance for (a) carcass weight, (b) conformation, and (c) fat, in heifers (– – –), steers (•••) and young bulls (——). Standard errors of residual variance estimates ranged from 6.50 to 22.50 (kg^2) for carcass weight, 0.02 to 0.03 ($units^2$) for conformation and 0.01 to 0.03 ($units^2$) for fat. Carcass conformation and fat scores were measured on a scale of 1-15.

Table 1. Numerical values on a 15-point scale in classification units given to carcass conformation class and carcass fatness class scores using a 15-, 7-, or 5-point scale*

Conformation class scale			Fatness class scale		
15 point scale[1]	5 point scale	Numeric value	15 point scale[2]	7 point scale	Numeric value
E+		15	5+	5	15
E=	E	14	5=		14
E-		13	5-		13
U+		12	4+	4H	12
U=	U	11	4=		11
U-		10	4-	4L	10
R+		9	3+		9
R=	R	8	3=	3	8
R-		7	3-		7
O+		6	2+		6
O=	O	5	2=	2	5
O-		4	2-		4
P+	P+	3	1+		3
P=	P-	2	1=	1	2
P-	P-	1	1-		1

[1]E+ is the best conformation; P- is the worst conformation.
[2]5+ is the fattest; 1- is the leanest.
* Hickey et al. (2007).

Table 2. Numbers of heifer, steer, and young bull records, in each residual variance class group.

Class (days)	Heifers	Steers	Young Bulls
360-400	566	162	1,399
401-440	1,293	374	3,979
441-480	1,937	582	8,051
481-520	2,790	753	9,724
521-560	4,700	1,293	10,288
561-600	7,791	1,936	12,316
601-640	11,202	3,058	13,083
641-680	16,414	6,460	13,405
681-720	20,151	13,113	13,844
721-760	17,552	19,681	N/A
761-800	11,718	18,329	N/A
801-840	8,069	13,202	N/A
841-880	6,665	10,821	N/A
881-920	5,719	12,096	N/A
921-960	2,637	7,027	N/A
961-1000	1,971	5,046	N/A
1,001-1,040	1,575	3,742	N/A
1,041-1,080	1,274	2,916	N/A
1,081-1,120	991	2,137	N/A
1,121-1,160	709	1,205	N/A
1,161-1,200	490	708	N/A

N/A= not applicable

Table 3. Mean, standard deviation (s.d.) and coefficient of variation (CV) for each gender for each carcass trait and age at slaughter.

Gender	Trait	Mean	s.d.	CV%
Heifers	Carcass weight (kg)	297.65	45.27	15.20
n=126,214	Conformation[1]	7.53	1.85	24.56
	Fat[2]	7.26	1.85	25.48
	Age at slaughter (days)	725.20	134.51	18.55
Steers	Carcass weight (kg)	346.72	53.15	15.41
n=124,641	Conformation[1]	6.35	2.25	35.43
	Fat[2]	6.67	1.85	27.73
	Age at slaughter (days)	810.26	129.45	15.98
Young bulls	Carcass weight (kg)	368.71	64.84	17.58
n=86,089	Conformation[1]	8.80	2.62	29.77
	Fat[2]	5.27	0.99	18.77
	Age at slaughter (days)	583.12	87.61	15.02

[1]Scored on a 15 point scale 1 (worst) to 15 (best).
[2]Scored on a 15 point scale 1 (lean) to 15 (fat).
n = number of animals in each gender.

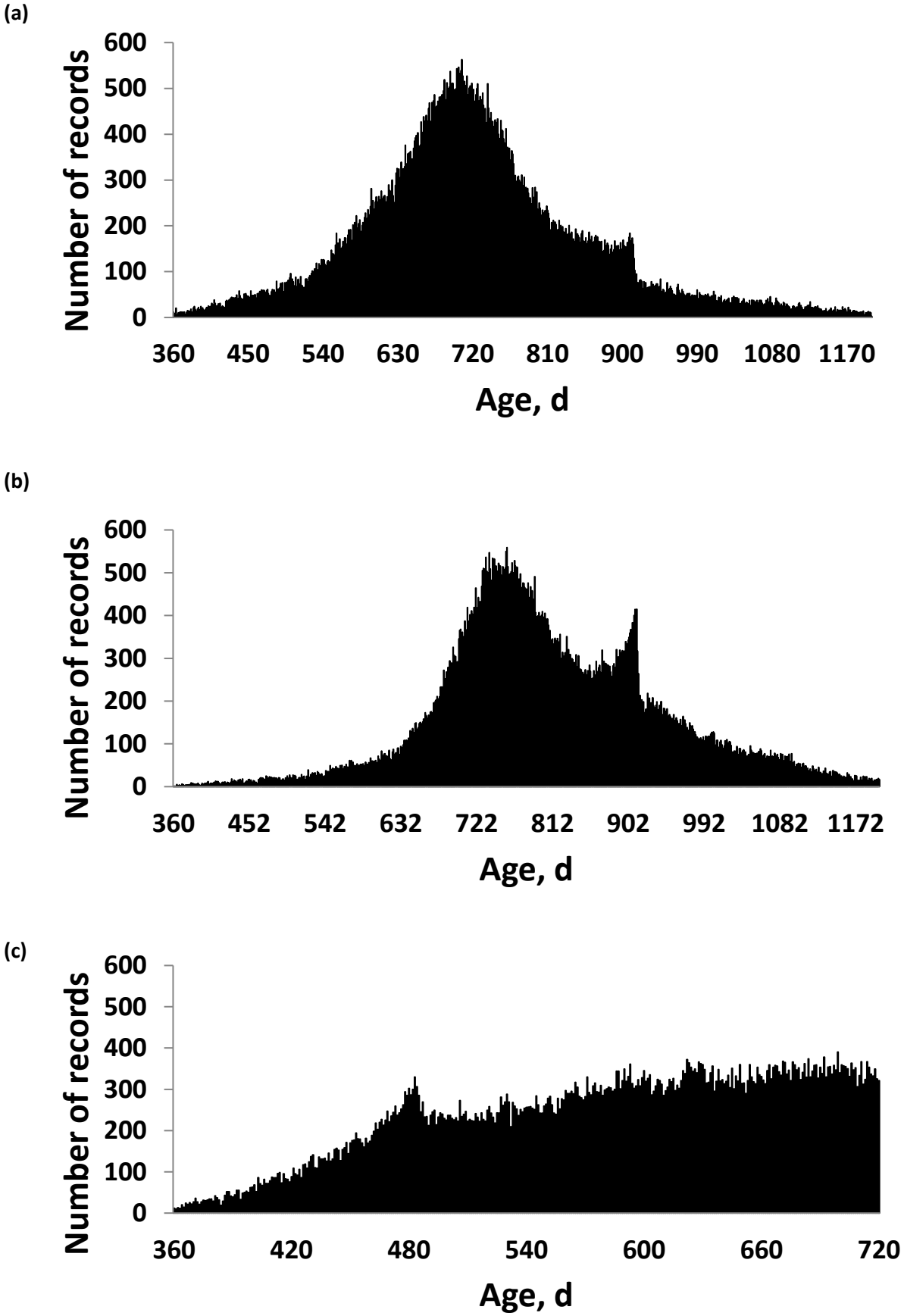

(a)
Number of records
600
500
400
300
200
100
0
360 450 540 630 720 810 900 990 1080 1170
Age, d
(b)
Number of records
600
500
400
300
200
100
0
360 452 542 632 722 812 902 992 1082 1172
Age, d
(c)
Number of records
600
500
400
300
200
100
0
360 420 480 540 600 660 720
Age, d

Figure 1.

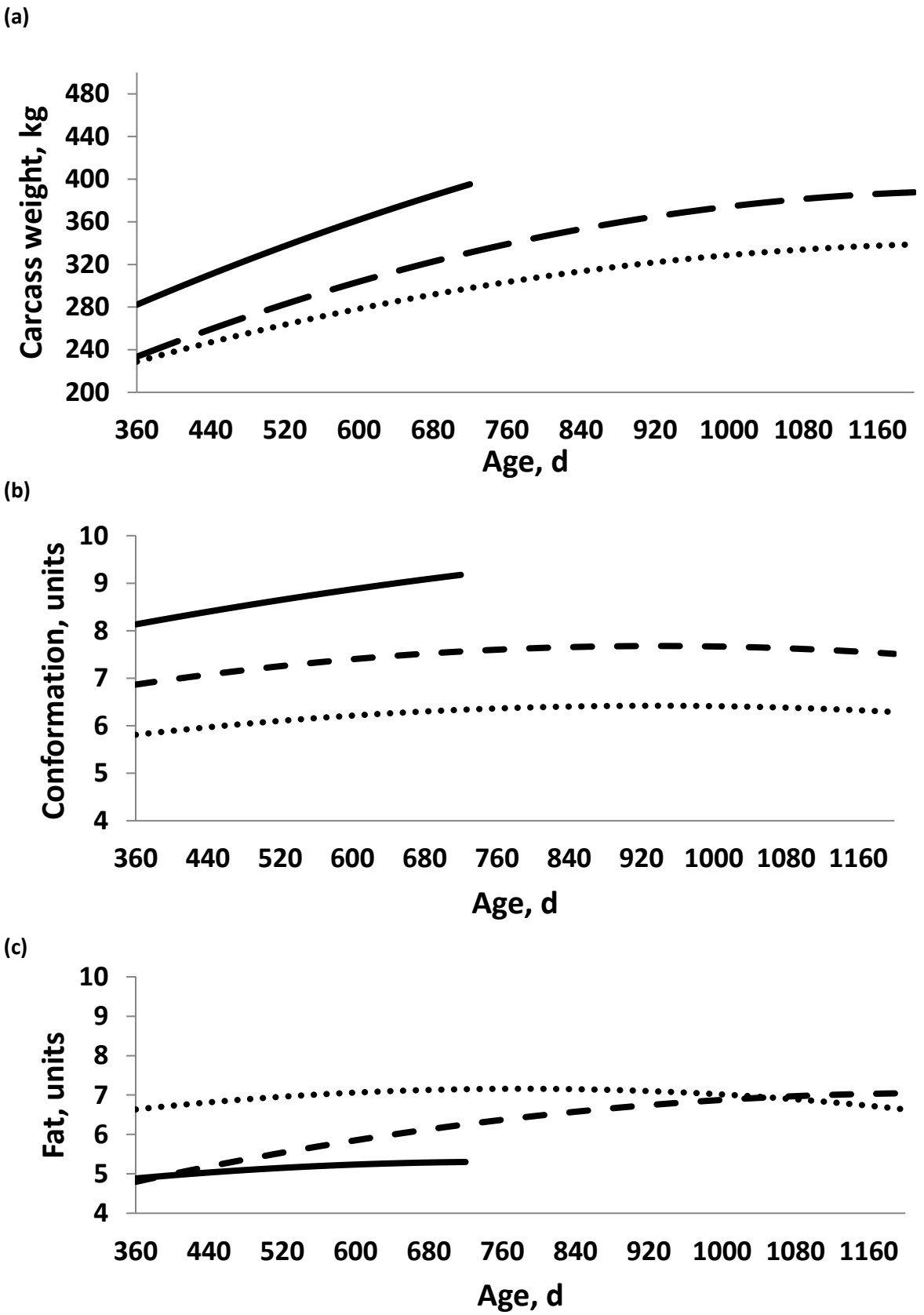

(a)
Carcass weight, kg
480
440
400
360
320
280
240
200
360 440 520 600 680 760 840 920 1000 1080 1160
Age, d
(b)
Conformation, units
10
9
8
7
6
5
4
360 440 520 600 680 760 840 920 1000 1080 1160
Age, d
(c)
Fat, units
10
9
8
7
6
5
4
360 440 520 600 680 760 840 920 1000 1080 1160
Age, d

Figure 2.

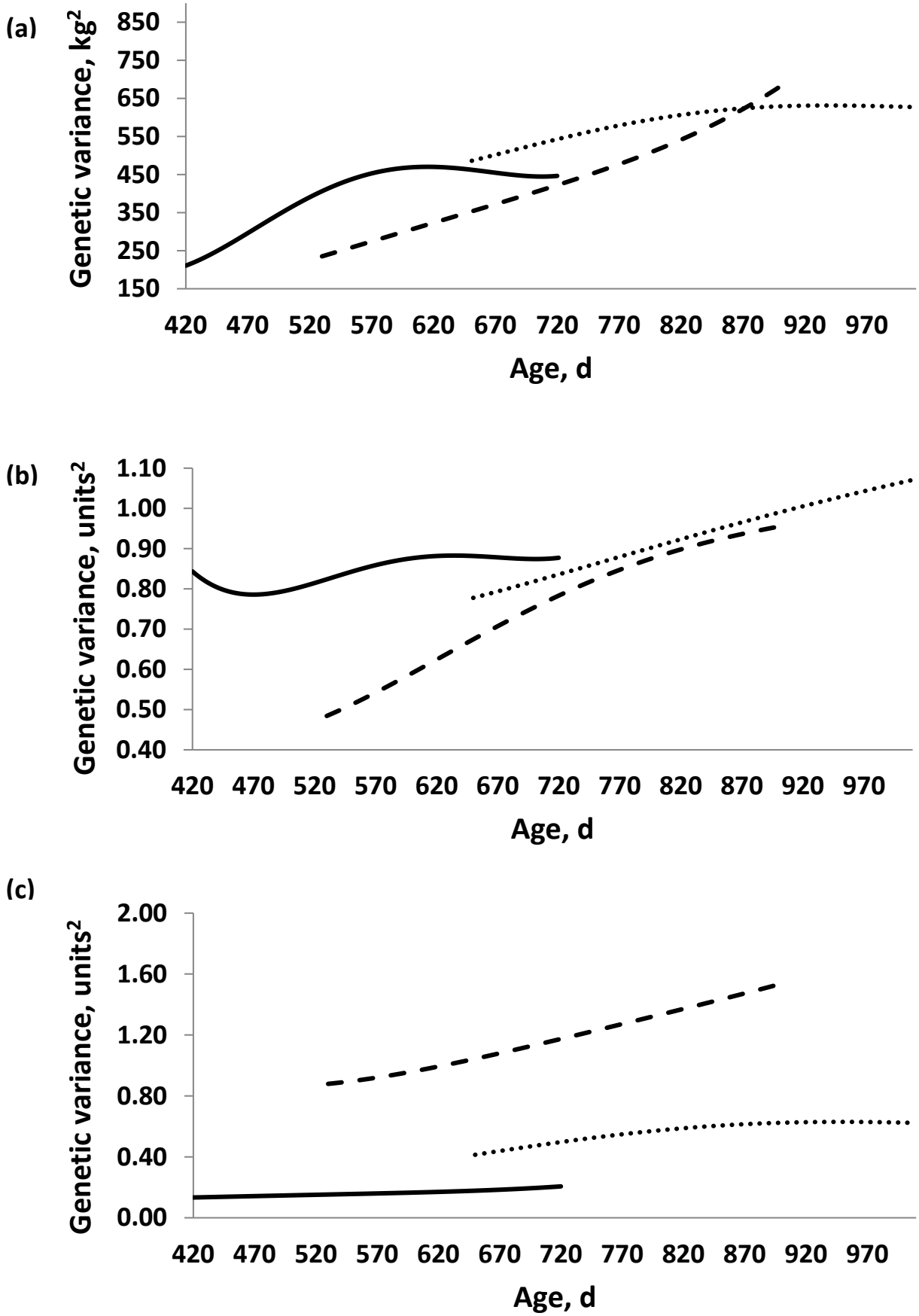

(a)
Genetic variance, kg²
850
750
650
550
450
350
250
150
420 470 520 570 620 670 720 770 820 870 920 970
Age, d
(b)
Genetic variance, units²
1.10
1.00
0.90
0.80
0.70
0.60
0.50
0.40
420 470 520 570 620 670 720 770 820 870 920 970
Age, d
(c)
Genetic variance, units²
2.00
1.60
1.20
0.80
0.40
0.00
420 470 520 570 620 670 720 770 820 870 920 970
Age, d

Figure 3.

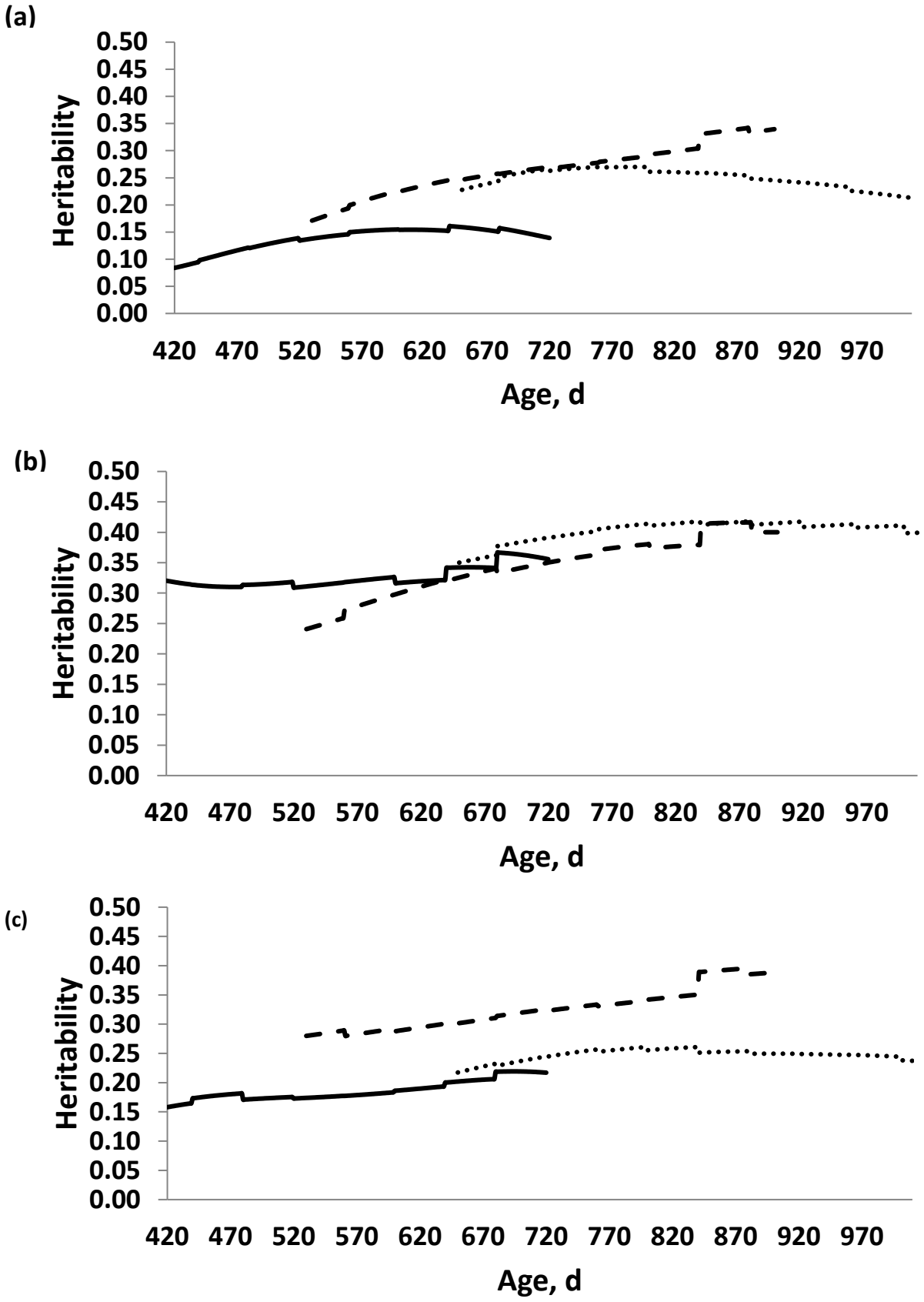
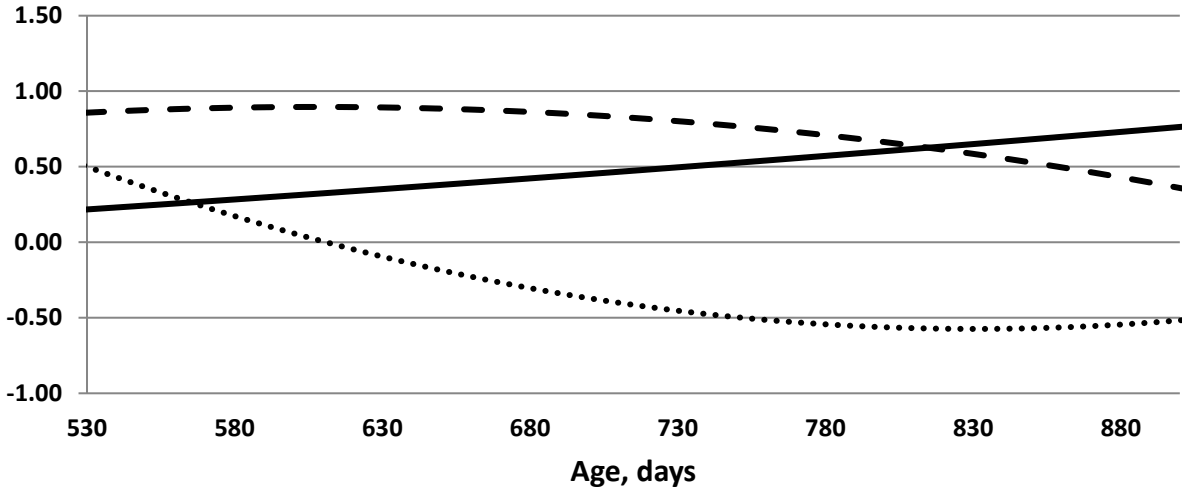
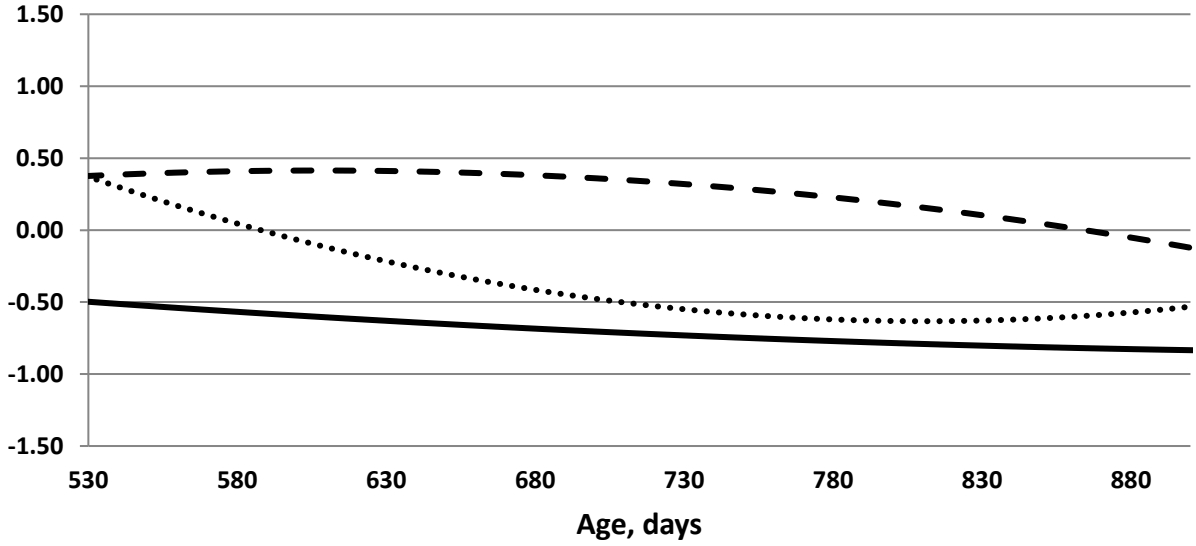

(a)
Heritability
0.50
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
420 470 520 570 620 670 720 770 820 870 920 970
Age, d
(b)
Heritability
0.50
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
420 470 520 570 620 670 720 770 820 870 920 970
Age, d
(c)
Heritability
0.50
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
420 470 520 570 620 670 720 770 820 870 920 970
Age, d

Figure 4.

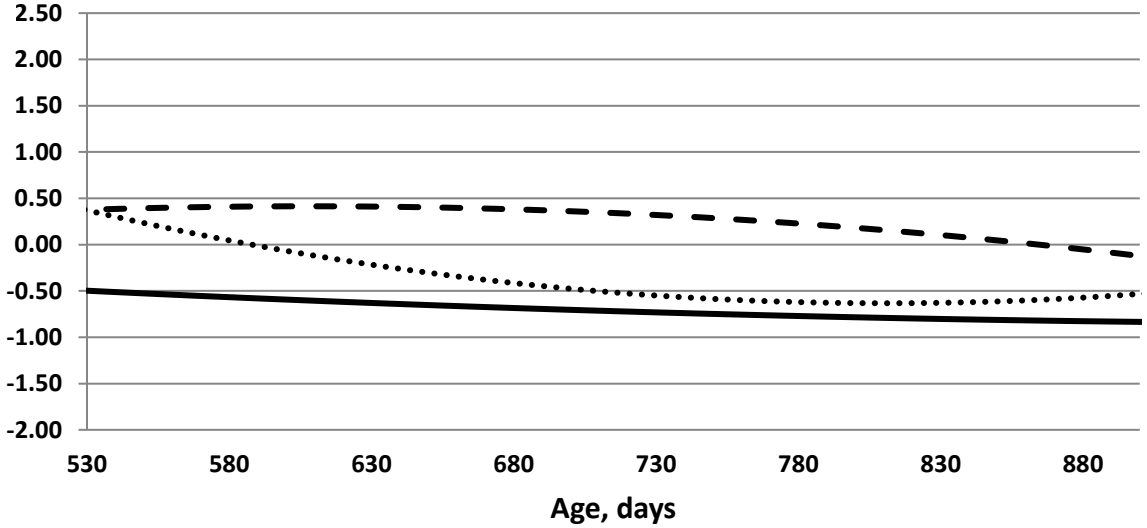
(a)


1.50
1.00
0.50
0.00
-0.50
-1.00
530
580
630
680
730
780
830
880
Age, days

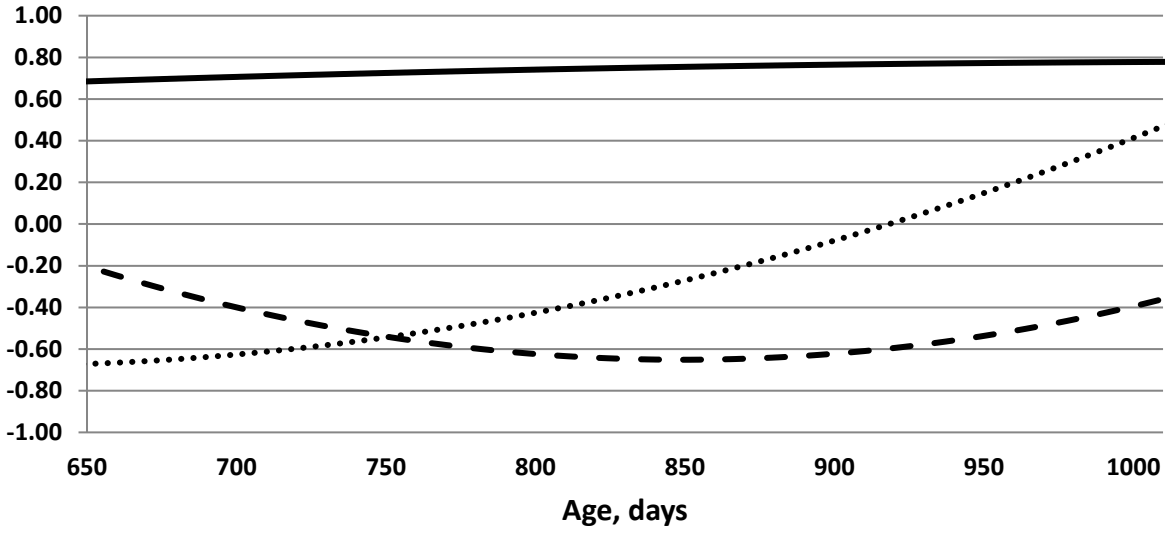
(b)


1.50
1.00
0.50
0.00
-0.50
-1.00
-1.50
530
580
630
680
730
780
830
880
Age, days

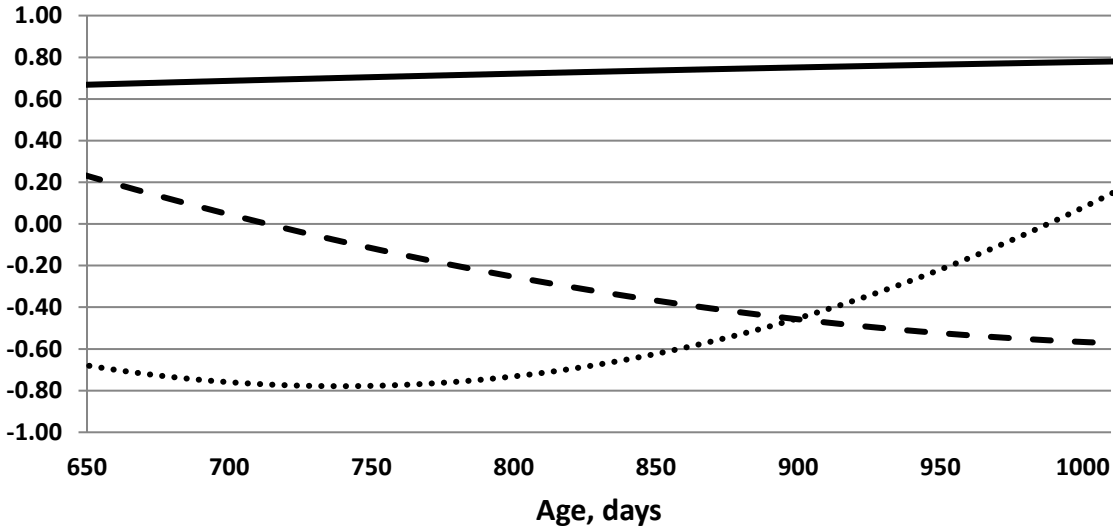
(c)


2.50
2.00
1.50
1.00
0.50
0.00
-0.50
-1.00
-1.50
-2.00
530
580
630
680
730
780
830
880
Age, days

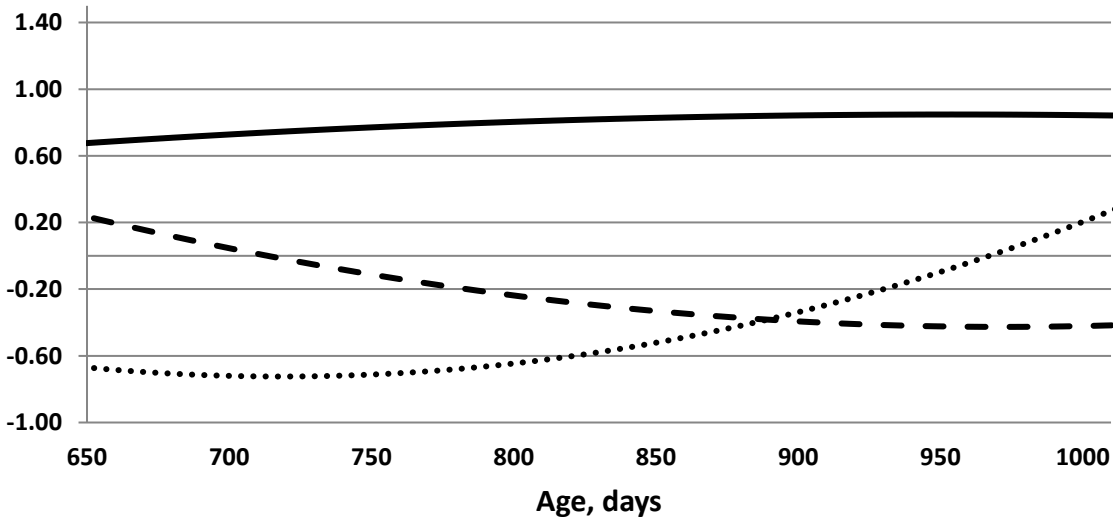
(d)

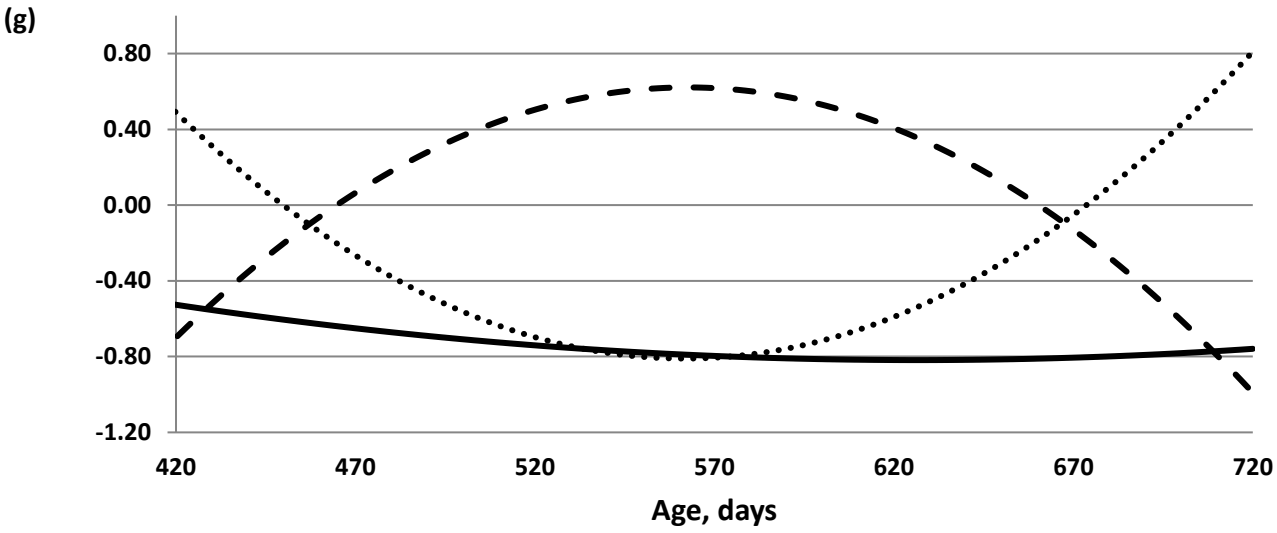

1.00
0.80
0.60
0.40
0.20
0.00
-0.20
-0.40
-0.60
-0.80
-1.00
650
700
750
800
850
900
950
1000
Age, days

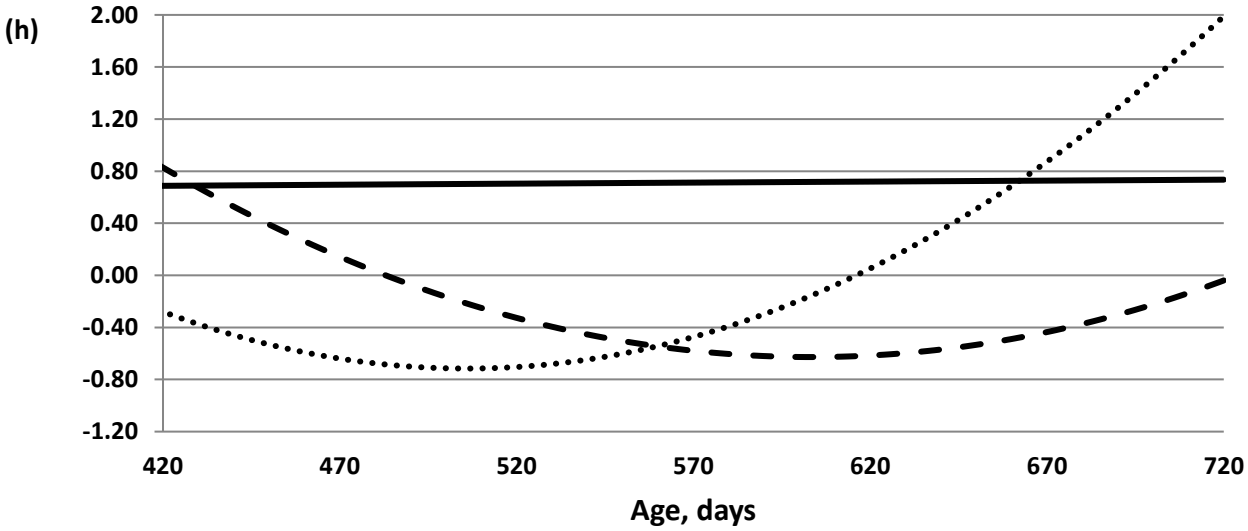
(e)


1.00
0.80
0.60
0.40
0.20
0.00
-0.20
-0.40
-0.60
-0.80
-1.00
650
700
750
800
850
900
950
1000
Age, days

(f)


1.40
1.00
0.60
0.20
-0.20
-0.60
-1.00
650
700
750
800
850
900
950
1000
Age, days


(g)
0.80
0.40
0.00
-0.40
-0.80
-1.20
420
470
520
570
620
670
720
Age, days


(h)
2.00
1.60
1.20
0.80
0.40
0.00
-0.40
-0.80
-1.20
420
470
520
570
620
670
720
Age, days

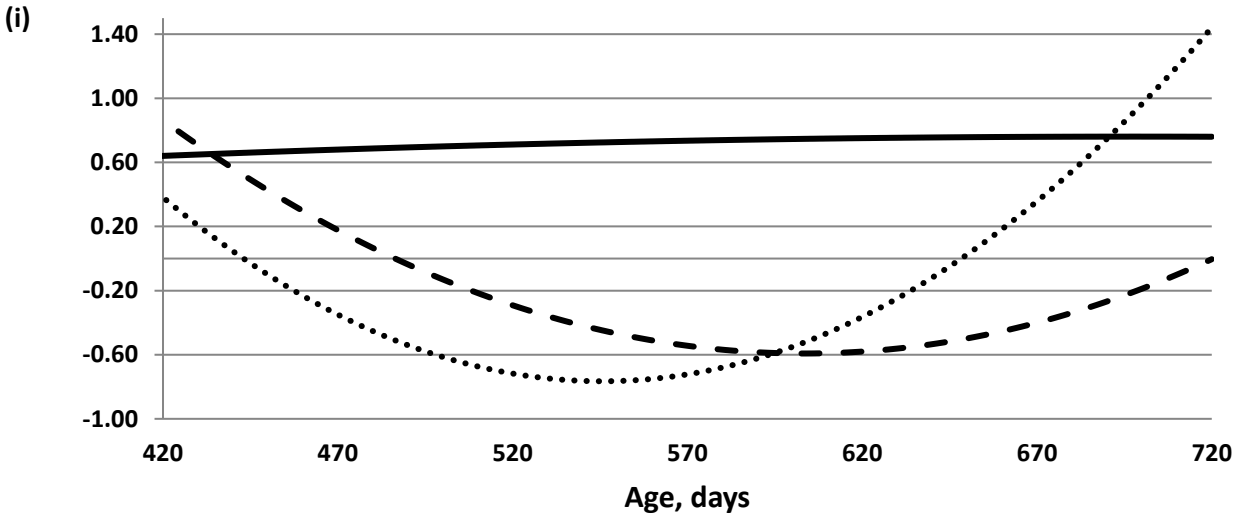

(i)
1.40
1.00
0.60
0.20
-0.20
-0.60
-1.00
420
470
520
570
620
670
720
Age, days

Figure 5.

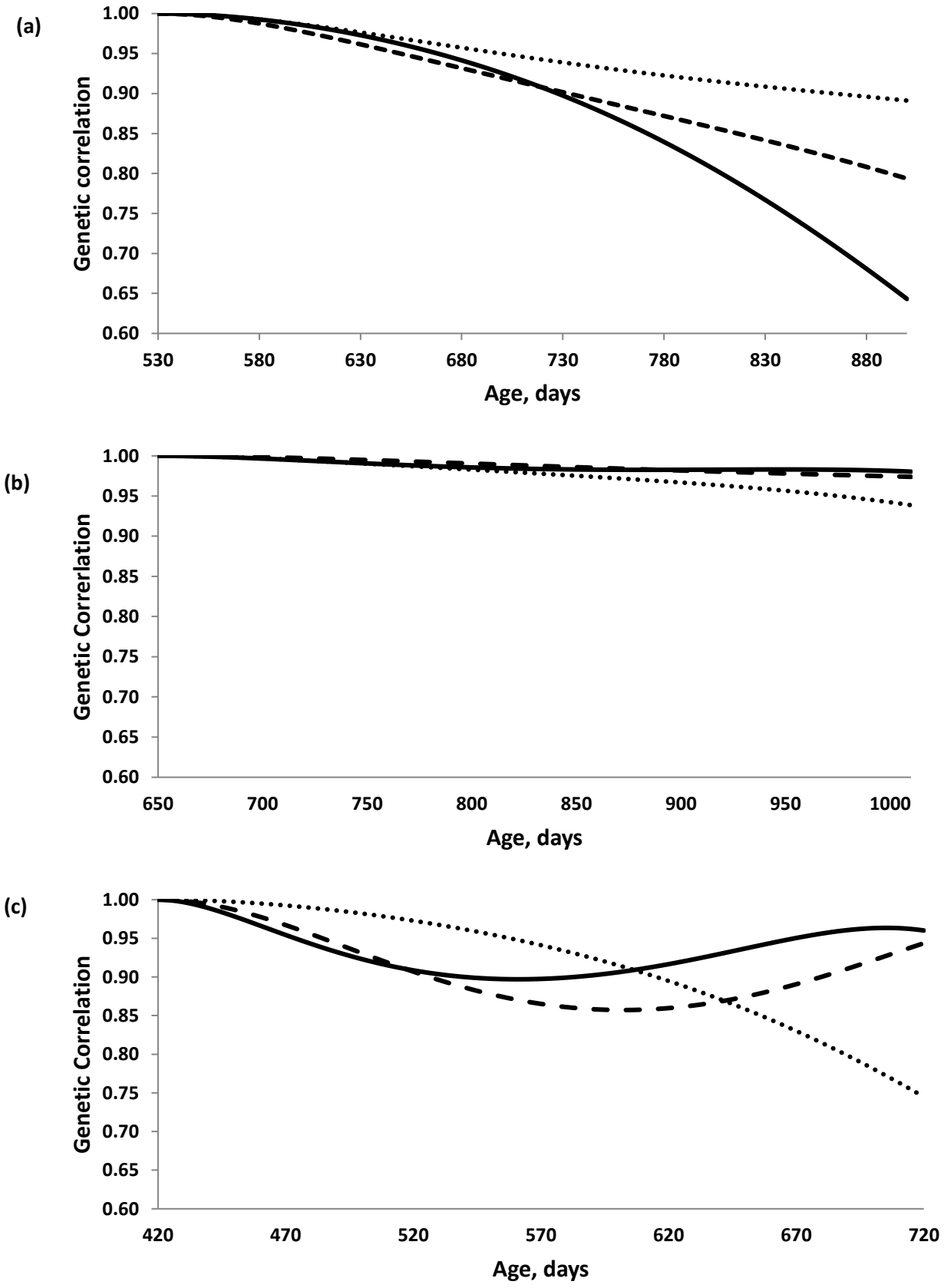

(a)
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0.65
0.60
Genetic correlation
530
580
630
680
730
780
830
880
Age, days
(b)
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0.65
0.60
Genetic Correrlation
650
700
750
800
850
900
950
1000
Age, days
(c)
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0.65
0.60
Genetic Correlation
420
470
520
570
620
670
720
Age, days

Figure 6.

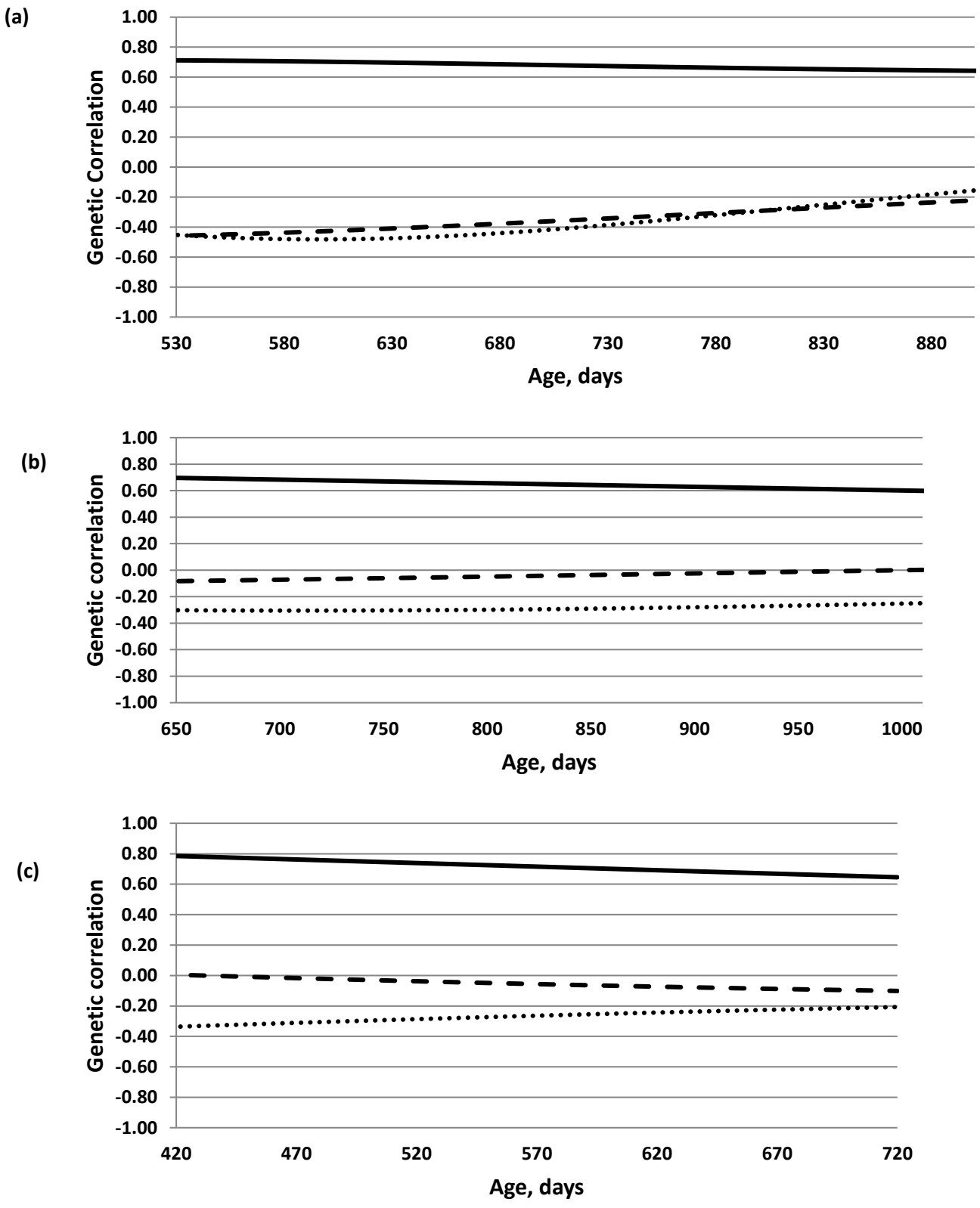

(a)
1.00
0.80
0.60
0.40
0.20
0.00
-0.20
-0.40
-0.60
-0.80
-1.00
Genetic Correlation
530
580
630
680
730
780
830
880
Age, days
(b)
1.00
0.80
0.60
0.40
0.20
0.00
-0.20
-0.40
-0.60
-0.80
-1.00
Genetic correlation
650
700
750
800
850
900
950
1000
Age, days
(c)
1.00
0.80
0.60
0.40
0.20
0.00
-0.20
-0.40
-0.60
-0.80
-1.00
Genetic correlation
420
470
520
570
620
670
720
Age, days

Figure 7.

Figure 1. Distribution of age at slaughter for (a) heifers, (b) steers and (c) young bulls.

Figure 2. Fixed effects profiles for (a) carcass weight, (b) carcass conformation and (c) carcass fat for heifers (−−−), steers (•••) and young bulls (──), estimated using quadratic polynomials. Intercept was taken as the weighted average of contemporary group and abattoir-date of slaughter and fixed effects from a fifth parity dam with no heterosis or recombination loss. Carcass conformation and fat scores were measured on a scale of 1-15.

Figure 3. Estimates of genetic variance for (a) carcass weight, (b) conformation, and (c) fat, in heifers (−−−), steers (•••) and young bulls (──). Standard errors of genetic variance estimates ranged from 20.72 to 67.57 (kg^2) for carcass weight, 0.04 to 0.10 ($units^2$) for conformation and 0.01 to 0.09 ($units^2$) for fat. Carcass conformation and fat scores were measured on a scale of 1-15.

Figure 4. Heritability estimate for (a) carcass weight, (b) conformation, and (c) fat, in Heifers (−−−), steers (•••) and young bulls (──). Standard errors of heritability estimates ranged from 0.01 to 0.02 for carcass weight, 0.01 to 0.03 for conformation and 0.01 to 0.03 for fat.

Figure 5. Eigenfunctions (y-axis unit less) associated with the largest (──), middle (−−−) and smallest (•••) eigenvalues in heifers for a) carcass weight, b) conformation and c) fat, and in steers, for d) carcass weight, e) conformation, and f) fat and in young bulls for g) carcass weight, h) conformation and i) fat.

Figure 6. Genetic correlations in a) heifers, b) steers and c) young bulls, between observations across ages at slaughter for carcass weight (—), conformation (– – –) and fat (•••). Standard errors of genetic correlation estimates ranged from 0.00 to 0.02 for carcass weight, 0.00 to 0.01 for conformation and 0.00 to 0.01 for fat.

Figure 7. Genetic correlations across age for (a) heifers (b) steers, and (c) young bulls, between carcass weight and conformation score (—), conformation and fat score (– – –), and fat score and carcass weight (•••) across ages at slaughter. Standard errors of genetic correlation estimates ranged from 0.01 to 0.04 for carcass weight and conformation score, 0.02 to 0.09 for conformation and fat score, and 0.02 to 0.14, carcass weight and fat score.